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# Infected or informed? Social structure and the simultaneous transmission of information and infectious disease

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# Infected or informed? Social structure and the simultaneous transmission of information and infectious disease


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# Abstract

Social interactions present opportunities for both information and infection to spread through populations. Social learning is often proposed as a key benefit of sociality, while disease epidemics are proposed as a major cost. Multiple empirical and theoretical studies have demonstrated the importance of social structure for the transmission of either information or harmful pathogens and parasites, but rarely in combination. We provide an overview of relevant empirical studies, discuss differences in the transmission processes of infection and information, and review how these processes have been modelled. Finally, we highlight ways in which animal social network structure and dynamics might mediate the trade-off between the sharing of information and infection. We reveal how modular social network structures can promote the spread of information and mitigate against the spread of infection relative to other network structures. We discuss how the maintenance of long-term social bonds, clustering of social contacts in time, and adaptive plasticity in behavioural interactions, all play important roles in influencing the transmission of information and infection. We provide novel hypotheses and suggest new directions for research that quantifies the transmission of information and infection simultaneously across different network structures to help tease apart their influence on the evolution of social behaviour.

**Key words:** social network, epidemic, social learning, social evolution, group-living, dynamic network

# Introduction

The diversity of social systems in animals is shaped by differences among populations in the costs and benefits of different types of social interaction (Krause, et al. 2002). The sharing of information provides one key benefit that improves fitness of more sociable individuals (Dall, et al. 2005, Danchin, et al. 2004), while the risk of acquiring pathogens or parasites (collectively referred to as “parasites” from here onwards) represents an important cost of sociality (Ezenwa, et al. 2016b, Ezenwa, et al. 2018, Krause, et al. 2002). While extensive work has been carried out examining the role of social interactions in information spread and infectious disease independently, the potential interactions and trade-offs between them has only recently started to be considered (Romano, et al. 2020). An important future challenge in evolutionary ecology will be to identify whether, and how, natural selection might favour social structures that can simultaneously optimise information-sharing and reduce the spread of infection in social species (Romano, et al. 2020). The solution to this evolutionary problem will depend on the differences in transmission dynamics between information and infection.

Social network analyses and modelling are increasingly used to study animal social behaviour, and these approaches have greatly benefitted research into the spread of parasites (Godfrey 2013, VanderWaal, et al. 2016)and information (Firth 2020) in wild animals. Interactions with more individuals result in increased opportunities for parasite transmission, while simultaneously making it possible for information to proliferate within a group or population. When an infection is present, the interplay between infection and information may lead to both long- and short-term changes in social structures, which can affect both individual fitness and entire populations (Pelletier, et al. 2009, Shizuka, et al. 2019). However, studying the trade-off between efficient information transmission and rapid spread of parasites is challenging due to the difficulty of combining data that reveal infection status, and data that indicate information transmission. Consequently, while network studies have examined how social relationships impact the transmission of either infection or information separately, there has, until recently, been little consideration of the interplay between information and infection spread within animal social networks (Romano, et al. 2020). As technology and techniques are increasingly becoming available that facilitate empirical research and data-driven modelling on the co-dynamics of information spread, parasite transmission and social network structure, it is important to synthesise existing knowledge across disciplinary boundaries to identify key research questions and challenges. Theoretical models, not just in the field of behavioural ecology, but also in network science and epidemiology more broadly, can also be integrated to provide a rich source from which to generate predictions about the trade-off between infection and information, and how this trade-off may shape the evolutionary ecology of animal social systems.

Here we synthesise knowledge on the role of social networks in transmission of information and parasites and develop hypotheses regarding how animal social systems may be adapted to reconcile the trade-off between acquiring information and becoming infected by parasites. We briefly review studies examining the transmission of parasites and information in animal social networks. We then highlight potential differences between the transmission processes of information and infection that will mediate this trade-off. Finally, we discuss how social relationships may be adapted to optimise both types of transmission, integrating insights from the network modelling literature and through empirical work in natural populations. Throughout we emphasise new avenues of study into the flow of parasites and information through animal social networks to promote a better understanding of how these two important ecological processes affect each other.

# Parasite transmission in animal social networks

The transmission of parasites that cause infectious disease can happen directly via specific types of behavioural interaction or indirectly via the environment (e.g. an individual using a refuge that has been contaminated by an infectious individual) (White, et al. 2017). Many infections are endemic, persisting stably within a host population for a long period of time (Viana, et al. 2014). Others are emergent, acquired either from a long-term environmental reservoir or spilling over from alternative host species (Daszak, et al. 2000). Networks of spatial associations and behavioural interactions are now known to be closely associated with epidemiology in wild animal populations (e.g VanderWaal, et al. 2014, Weber, et al. 2013). Overall network structure is critical in determining how parasites spread through populations. For example, the presence of distinct social communities can limit the spread of infection in animal groups or populations (Griffin, et al. 2012, Sah, et al. 2017). Social network analysis can also help identify potential routes of transmission (Silk, et al. 2017a, White, et al. 2017), determines individual variation in transmission potential (VanderWaal, et al. 2016) and predicts or explains how infection spreads through populations (Craft 2015, Silk, et al. 2017b). Network analyses have also revealed associations between individual phenotypes, infection and network position. For example, European badgers *Meles meles* that test positive for bovine tuberculosis tend to have fewer connections to their own social group and more social connections with neighbouring groups (Weber, et al. 2013), and male-biased infection is associated with sex-differences in social network position (Silk, et al. 2018c).

Fine-scale social networks can be used to identify if and how different types of social interaction generate transmission opportunities. The most important type of contact for transmission may vary among systems: in some species direct social contacts may be more important than shared space use (Blyton, et al. 2014, VanderWaal, et al. 2014). More recently, the importance of cryptic contacts has been revealed in a mixed-species community of bats, with social networks based solely on the sharing of, or physical contact at, roosts not sufficient to capture fungal pathogen transmission dynamics (Hoyt, et al. 2018). Together these studies reveal that using social networks in disease ecology might help to identify potential transmission routes, but might be uninformative and potentially misleading if the types of social interactions modelled are not those that facilitate parasite spread.

Infection may lead to temporal changes to network structure by changing patterns of social behaviour (Ezenwa, et al. 2016a). Parasites often manipulate the host's social behaviour to facilitate further transmission (e.g. Berdoy, et al. 2000, Loot, et al. 2001, Randall, et al. 2006),while the social behaviour of the infected host and/or the individuals that interact with it might change to prevent spread, resulting in co-dynamics between parasite spread and network structure (Silk, et al. 2017a). In guppies *Poecilia reticulata* for example, infected individual are avoided by uninfected fish, making sick individuals less well connected and causing the networks to become less clustered overall (Croft, et al. 2011). At a network-level these behaviour-infection co-dynamics can have a protective effect. In ants, for example, social networks of infected colonies become more modular and assortative, resulting in them becoming less efficient in terms of information transmission capacity but more effective at limiting the spread of infection (Stroeymeyt, et al. 2018). It is clear then that variation in connectivity among individuals, the resultant network structure, and changes in network dynamics following infection, all have important implications for the emergence, spread and persistence of parasites in wildlife populations.

# Information transmission in animal social networks

Information can be acquired by sampling the environment (personal information; Dall, et al. 2005) or by observing or interacting with other individuals or their products (social information; Dall, et al. 2005, Danchin, et al. 2004). Individuals can spread social information inadvertently or can choose to deliberately transmit information via signals. A receiver must then decide whether to act on this information or not (Dall, et al. 2005, Schmidt, et al. 2010). The transfer of social information usually requires sensory contact between individuals and is therefore linked directly to spatial association and/or behavioural interactions. Consequently, as with parasite transmission, an individual's social network position causes variation in the probability and rate of receipt of information, and their contribution to the speed and quality of information transmission through a population (Firth 2020, Lusseau 2003, Lusseau, et al. 2004, Modlmeier, et al. 2014). Depending on the duration information is useful, an individual's network position will strongly influence how they can utilise this information. For example, information such as the discovery of a resource location (Aplin, et al. 2012, Blonder, et al. 2011, Webster, et al. 2013) may only be accurate for a short time if a resource is ephemeral or is rapidly depleted. A central network position or high level of connectivity to the individual who initially discovers such resources will be highly beneficial to potential recipients, as demonstrated in several studies of the influence of network position on food patch discovery in flocks of songbirds (Aplin, et al. 2015, Aplin, et al. 2012, Jones, et al. 2017, Tóth, et al. 2017). Therefore, when information-gathering is beneficial, group members may be attracted to individuals who regularly provide information, changing their position in the social network. In ring tailed lemurs *Lemur catta*, for example, this led to informed individuals occupying more central network positions (Kulahci, et al. 2018).

Social associations are also linked to the spread, through social learning, of behavioural innovations which can arise via trial and error learning (Allen, et al. 2013, Aplin, et al. 2014). Such innovations range from simply adopting a new foraging ground (Schakner, et al. 2017) to tool use (Coelho, et al. 2015, Hobaiter, et al. 2014, Mann, et al. 2012, St Clair, et al. 2015) or novel foraging techniques (Aplin, et al. 2014, Boogert, et al. 2014, Kendal, et al. 2010). Innovations of long-term value can be transmitted to subsequent generations (Aplin, et al. 2014, Cantor, et al.) and impact long-term social structure, provided individuals alter their social interactions to maximise their chances of acquiring information (Coelho, et al. 2015, Kulahci, et al. 2018). One possible outcome is that long-term, preferential associations with individuals who adopt the same behaviours (Mann, et al. 2012) will homogenise behavioural repertoires in any given group and can establish "animal cultures" (Allen, et al. 2013, Aplin, et al. 2014, Krützen, et al. 2005). For example, bottlenose dolphins *Tursiops spp.* using marine sponges as tools during foraging have been shown to preferentially associate with other tool users (Krützen, et al. 2005, Mann, et al. 2012). This behavioural homogenisation may, depending on initial network structure, increase connectedness which can lead to the structure of networks becoming more random. Alternatively, if networks are already divided into distinct social communities, these groups might become increasingly isolated from each other (Cantor, et al. 2013, Morgan, et al. 2012).

Generally, the transmission of social information is considered to benefit the recipient individuals. However, there is potential for information transmitted to be outdated, poor, corrupted or misleading (Klein, et al. 2018, Koops 2004, Preece, et al. 2014, Schmidt, et al. 2010, Ward, et al. 2008). While such information might simply result in wasted time and energy (Dall, et al. 2005, Giraldeau, et al. 2002, Preece, et al. 2014), more severe costs are possible depending on the value of accurate information (Koops 2004, Nocera, et al. 2005, Rieucau, et al. 2011). For example, inexperienced bobolinks *Dolichonyx oryzivorus* relying on social information to make breeding habitat choices were found to settle in and defend sub-optimal territories in response to misleading information (Nocera, et al. 2005). The spread of misinformation through a network could have impacts on fitness that resemble the spread of parasites (Laland, et al. 1998, Ward, et al. 2008). When learning how to solve problems, individuals commonly show strong preference for the first solution to which they are exposed (e.g. birds: Aplin, et al. 2014, fish: Laland, et al. 1998). In competitive situations, recipients of suboptimal information might lose out to better informed individuals or successful innovators. While the spread of misinformation has not yet been the subject of empirical study using network techniques, there is strong potential for it to be important in nature. Similar to parasites, misinformation may be more likely to spread through a population if an individual transmitting misinformation is highly central to the social network, as information from these individuals may be more likely to be utilised by others, and their central position provides more transmission opportunities (Firth 2020, Giraldeau, et al. 2002, Ward, et al. 2008).

# Differences between information and parasite transmission

We have illustrated the importance of an individual's social connections both in their access to and sharing of information, and in their exposure to and onward transmission of parasites. This suggests that animal societies might suffer a direct trade-off between the transmission of information and parasites. However, there are important general (though not universal) distinctions between the two transmission processes (Table 1).

Table 1: Summary of the general key differences in mechanisms and consequences of information and parasite transmission.

| | Infection | Information |
|---|---|---|
| Transmitter decisions | Individuals inadvertently infect others (though parasites might change host behaviour to facilitate infection). | Individuals can inadvertently inform others (e.g. through cues/eavesdropping) or choose to deliberately inform others (e.g. signals). |
| Receiver decisions | Recipients of parasites cannot choose whether they become infected or not. | Individuals decide whether to alter their behaviour based on the information received. |
| Number of transmitters | The probability of infection depends directly on the absolute magnitude of exposure. The number of simultaneously infected associates does not affect per- contact likelihood of infection. | The probability of accepting information can depend on the relative magnitude of exposure to transmitters and non-transmitters. The proportion and phenotypic traits of associates transmitting information can influence whether an individual uses information received (i.e. social learning strategies). |
| Social relationships | Prior social relationships have no effect on the per-contact likelihood of infection. | Prior social relationships can influence whether an individual adopts information received. |
| Transmission vectors | Parasites spread mainly through direct physical contact or close proximity, or via shared use of environmental reservoirs. | Information spread does not tend to require physical contact and can potentially occur via long-range sensory interactions. |
| Heterospecific transmission | Parasites can spread between species, though this may require adaptation by the parasite. | Information can spread between species. Receiver may require adaptation or learning to utilise information from heterospecifics. |
| Selection | Selection acts on both the host and the parasites they transmit. | Selection acts on the information transmitter and receiver, but only indirectly on the information being transmitted. |
| Behavioural changes | Infected individuals are often avoided by group members, and become less well-connected in the social network. Infections might manipulate host behaviour to increase probabilities of onward transmission. | Informed individuals can be desirable to associate with, and become better connected in the social network. |

Most importantly, information transmission will typically involve choice, sometimes for a transmitter, who can choose when to transmit information and to whom, and always for the receiver, who chooses whether to alter their behaviour based on the information. Choice by the receiver means that the social transmission of information does not necessarily depend on a simple probability of transmission associated with each interaction (Bakshy, et al. 2009, Jackson, et al. 2013). Individuals may require multiple exposures to a transmitter, or require a certain proportion of social connections to be transmitting before choosing to utilise a piece of information (Bakshy, et al. 2009, Jackson, et al. 2013). For example, chimpanzees were more likely to acquire a behaviour if it was demonstrated by three different individuals than when it was demonstrated three times by a single individual (Haun, et al. (2012). Evidence for such social conformity, where naïve individuals disproportionally copy the behaviour demonstrated by the majority of conspecifics, has also been reported for mate-choice copying in fruit flies (Nöbel, et al. 2018) and great tits solving puzzle boxes in the wild (Aplin, et al. 2015). This information transmission process differs from parasite transmission where a) the risk of acquiring infection rises monotonically with the duration and/or number of contacts with infected individuals, and b) having multiple infected social connections presents more opportunities for contact with infected individuals, but does not alter the per-interaction probability of infection. Therefore, in species showing conformist social learning strategies, the acceptance of information depends on the relative magnitude of exposure to transmitters and non-transmitters of information in a frequency-dependent manner, and similar non-linear changes in the likelihood of transmission can also occur for other social learning strategies.

Another key difference between information and infection is the effect that prior social associations can have on the likelihood of transmission. The current and previous social relationships of an individual can directly impact the probability of using information acquired through a particular social interaction. This phenomenon was first coined “directed social learning” (Coussi-Korbel, et al. 1995) and later described as one of many potential “social learning strategies” (Laland 2004). Some of the clearest evidence of such a “Whom to learn from” social learning strategy comes from the importance of familiarity for the rate of social learning in many species (e.g. Kavaliers, et al. 2005, Swaney, et al. 2001). Information from a familiar individual may result in an immediate change in behaviour, whereas an animal may require more exposures to a piece of information if the source is unfamiliar. Transmitter familiarity is one of several relationship traits that might influence the decision to use a piece of information, with traits such as relatedness or social rank also potentially important (Boogert, et al. 2018, Evans, et al. 2018, Farine, et al. 2015b, Kavaliers, et al. 2005, Radford 2004, Valsecchi, et al. 1996). Relationship traits can also interact with the ambiguity of transmitted information (Ward, et al. 2008) and the phenotype of the transmitter, such as their experience (McComb, et al. 2001) or obvious fitness cues (Toth, et al. 2011), to shape the likelihood of information being used. Similarly, it is possible for prior social relationships with other group members to have a profound effect on the health of individuals in social species (Sapolsky 2005), and the social buffering hypothesis (Ezenwa, et al. 2016b) proposes that positive social relationships can increase resistance to, and tolerance of, infection in group-living species (e.g. Almberg, et al. 2015, Balasubramaniam, et al. 2016, Ezenwa, et al. 2018, Scharf, et al. 2012, Walker, et al. 2009). However, unlike the spread of information, this is a general effect and specific prior relationships with infected individuals do not influence the transmission process in the same way that prior relationships with informed individuals do.

Another important consideration is *how* information and infection are transmitted. Social information can be transmitted in multiple ways (Blanchet, et al. 2010, Danchin, et al. 2004), which may require prolonged or close interactions (e.g. the waggle dance in bees; Von Frisch 1967, Ward, et al. 2008), may be possible with much looser associations (e.g, auditory cues; Hollen, et al. 2009), or may be transmitted indirectly via environmental signals or cues (e.g, scent marking: Gosling, et al. 2001). Conversely, parasites are likely to be transmitted through a different set of interactions, such as prolonged close contact that facilitates aerosol transmission (Delahay, et al. 2001); shared use of environmental reservoirs of parasites (Godfrey, et al. 2009); aggressive interactions or mating (Hamilton, et al. 2019). The extent of the overlap in the types of social interaction that expose individuals to either information or infection will be important in determining the costs and benefits of being central in different types of social network.

Both parasites and information can be transmitted between as well as within species. The spillover of parasites will typically depend on ecological opportunity provided by the frequency of direct and/or indirect (epidemiologically relevant) contacts between members of the different species (Faust, et al. 2018, Plowright, et al. 2017, Woolhouse, et al. 2001), the phylogenetic similarity of potential hosts (Kreuder Johnson, et al. 2015, Longdon, et al. 2011) and the evolvability of the parasite – parasites with higher mutation rates (e.g. some viruses) can infect a larger range of different host species (Kreuder Johnson, et al. 2015, Woolhouse, et al. 2001). As with parasite transmission, information transmission is also more likely to occur between closely related species (Coolen, et al. 2003, Dawson, et al. 2012, Farine, et al. 2015a, Goodale, et al. 2010, Goodale, et al. 2008, Seppänen, et al. 2007), often an outcome of them having similar information requirements due to sharing ecological challenges (though see: Anne, et al. 1983, Lilly, et al. 2019, Whiting, et al. 1999, for transfer between less related species). An animal's ability to utilise information from heterospecifics will also depend on the type of information. For example, seeing a heterospecific fleeing from a predator and using this as information about a potential threat is relatively simple, requiring no advanced learning processes or adaptation. However, using a heterospecific alarm call to assess threat may require prior experience with the calling species, so as to learn the association between the alarm call and threat (Ferrari, et al. 2008, Magrath, et al. 2015, Templeton, et al. 2007). As a result, the type and quality of information passed between species can be highly variable across contexts and species, and rates of social learning can differ between conspecific and heterospecific relationships (Farine, et al. 2015a, Goodale, et al. 2008).

A final important distinction between information and parasite transmission is that the former is the subject of selection only on the host population, while the latter depends on selection on both the host and the parasite being transmitted. For example, individuals that acquire novel social information may develop new social associations and become more central within a social network (Kulahci, et al. 2018), which may benefit both themselves and other group members, especially in highly related groups. This is in direct contrast to transmission of infection, where group members would be expected to avoid contact with infected individuals (Croft, et al. 2011, Stephenson, et al. 2018), which can lead *un*infected individuals to become more central as a result of parasite spread (Shaw, et al. 2008). A key component of this difference between infection and information is that there is often antagonistic selection on sickness behaviours between hosts and their parasites, whereby hosts will be selected to behave to avoid infecting (related) group members (Croft, et al. 2011, Lopes, et al. 2016), while parasites will be selected to cause host behaviours that maximise transmission (e.g. furious behaviour in rabid canines; Randall, et al. 2006)

The outcome of these differences between the transmission of infection and information is that while infection can be considered a simple contagion process, the spread of information is increasingly considered a complex contagion (Centola 2010, Macy 1991) affected by many of the social learning rules described above. Consequently, the spread of parasites has normally been modelled as a simple contagion using cascade models (Moore, et al. 2000), in which the probability of infection increases with increasing absolute exposure to infected individuals. In contrast, the transmission of information could be either a simple or complex contagion depending on the social learning rules used by individuals. As a result, the spread of information has been modelled using a variety of dose-response models, including simple cascades, threshold models (Kempe, et al. 2003), and hybrid cascade-threshold models (de Kerchove, et al. 2009) models (Fig. 1). The precise nature of the threshold, and whether it is a true threshold (deterministic), a stochastic transmission process with a threshold or a continuous dose-response curve, will depend on the social learning rules used. The measure of exposure used in these models might be relative exposure (conformist social learning in response to the prevalence of information among social contacts), absolute exposure (social learning in response to a minimum number of neighbours behaving in a particular way) or based on temporal rules (e.g. learning in response to a threshold number of interactions with informed individuals in a given time period). Variation in the status of informed individuals or their relationships to the focal individual could be key mechanisms which push the transmission process even further away from simple contagion.

# Using models to capture the differences between information and parasite transmission

The similarities and differences between information and parasite transmission can be captured using dynamic computational modelling tools (Fig. 1), such as compartmental models. Compartmental models consider the transition of individuals between states, with individuals in each state assumed to have the same characteristics (Stattner, et al. 2011). For example, a susceptible-infected-recovered (SIR) model (used commonly in epidemiology) contains three states: susceptible (or naïve) individuals; infected with a parasite (or exposed to and exploiting the information); and recovered individuals who are now immune to that infection (or who no longer use the information to inform their behaviour, see supplementary table 1). When applied to transmission through networks, compartmental models are typically applied as stochastic individual-based models, in which the transition of each individual between compartments is modelled separately and depends on the properties of their network connections. Such models are usually impossible to solve analytically (Craft 2015). These models avoid the assumption that populations mix freely, so that any individual will be able to infect any other individual in a population. General compartmental models applied to networks can be used to study parasite transmission (Tunc, et al. 2014, Volz 2008), information flow (Gurley, et al. 2016, Wang, et al. 2011), or both simultaneously (Juher, et al. 2015, Wu, et al. 2012). See supplementary Table 1 for many examples of simple compartmental models that can be applied to both information and parasite transmission, and those more suitable for detailed models of particular transmission types.

Cascade, threshold and hybrid compartmental models can all be adapted to capture system-specific nuances regarding the importance of transmitter identity, social history, and behaviours that change in response to exposure (Fig. 1). Cascade models are typically implemented as stochastic models, with each additional unit of social interaction associated with a linear increase in the risk of infection (Fig. 1a). True threshold models are deterministic with individuals moving between states following fixed rules that are determined by the states of their neighbours, and can be used to model strictly conformist social learning, for example. Hybrid models can be used to mix properties of either model, for example by introducing stochasticity to the threshold model or incorporating continuous dose-response curves. For example, the latter might be applicable to studying imperfect conformist social learning where changes in state are governed by the states of neighbouring individuals according to a sigmoidal function rather than a strict threshold (e.g. Fig. 1c).

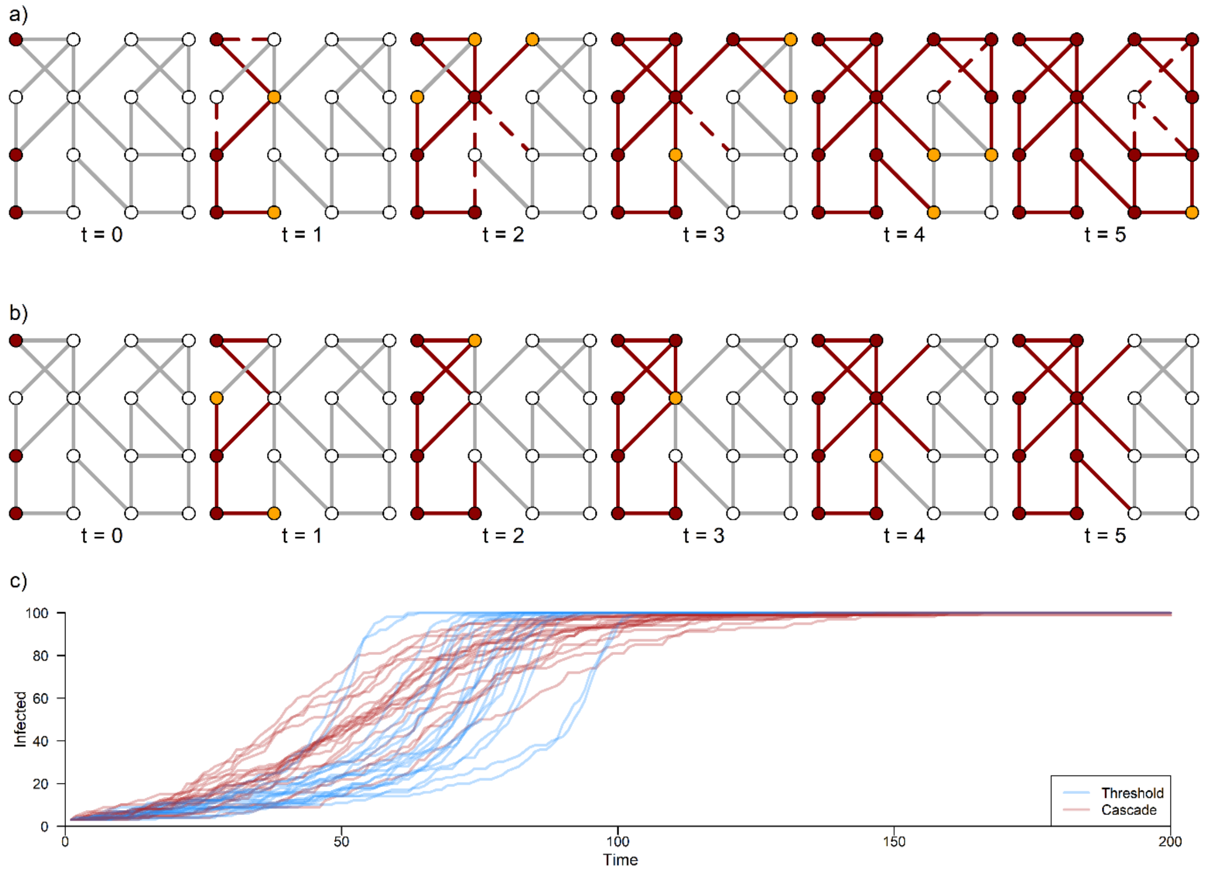


Figure 1. a) Example of a cascade model of simple contagion acting on an unweighted network (all individuals have an association strength of either 1 or 0) of 16 individuals over four time steps. Grey lines represent social associations, red nodes represent infected/informed individuals while yellow nodes represent individuals who will become infected/informed in the next time step. In this cascade model an infected/informed individual infects/informs each uninfected neighbour with a probability of 0.5 per time step. Solid red lines indicate an infected/informed node successfully infecting/informing a neighbour, while a dashed line represents a failure. If successful, the neighbour will become infected/informed in the next time step. b) A conformist transmission model (here a true threshold model, but a stochastic implementation would produce similar results) acting on the same network as a). Individuals become infected/informed when 50% of their neighbours are infected/informed. In this simulation, spread stalls at timestep 4 as there are not enough infected/informed individuals to result in transmission. c) Comparison between simple and conformist contagion models in a random network of 100 individuals, showing the percentage of the population infected over 200 arbitrary time-steps. For the simple contagion model there is a probability of 0.8% chance per time-step that infection is transmitted through an edge between an infected and susceptible individual. In the conformist model a sigmoid curve is fitted to the likelihood of an individual exploiting information with a baseline (asocial) individual learning rate of 0.2% per time-step, a maximum probability of learning of 30% per time-step and the threshold (pivot point of the sigmoid function) occurring at 50% of connected individuals providing information. Full R code for the model is provided in the Supplementary information.

# Social structure and the infection-information trade-off

In the following sections, we highlight ways in which animal social networks might reflect the outcome of selection acting on individuals to maximise their acquisition of beneficial information and minimise their risk of being infected by parasites. Specifically, we focus on the role of structural heterogeneity in social networks, temporal heterogeneity in interactions, responsive changes in social interactions and the role of different types of interaction. We integrate the extent of our current knowledge of animal social systems with insights from compartmental network models (Supplementary table 1) applied to theoretical and data-driven network structures in other disciplines.

### *Structural heterogeneity and transmission in animals*

The structure of contact networks is integral to transmission dynamics for cascade models (Moore, et al. 2000, Newman 2002) and threshold models (Alkemade, et al. 2005, Hodas, et al. 2014). We focus on three aspects of social network structure that have received considerable research interest and have clear applications to the study of animal societies: i) variation in connectivity among individuals causing networks to possess heterogeneous degree distributions (the extreme case being networks with scale-free properties), ii) modular structure that is characterised by densely connected regions (called communities) with rather few connections between these communities, and iii) small-world structure, which is best envisaged as individuals (or "nodes") being connected mostly with (spatial) neighbours, but possessing occasional contacts with much more distant nodes, resulting in transmission pathways through the network that are typically short compared to random or modular networks. We depict these different aspects of network structure in Fig. 2. Animal social structure is highly variable and can display one or multiple of the scale-free, small-world or modular properties introduced here (Wey, et al. 2008).

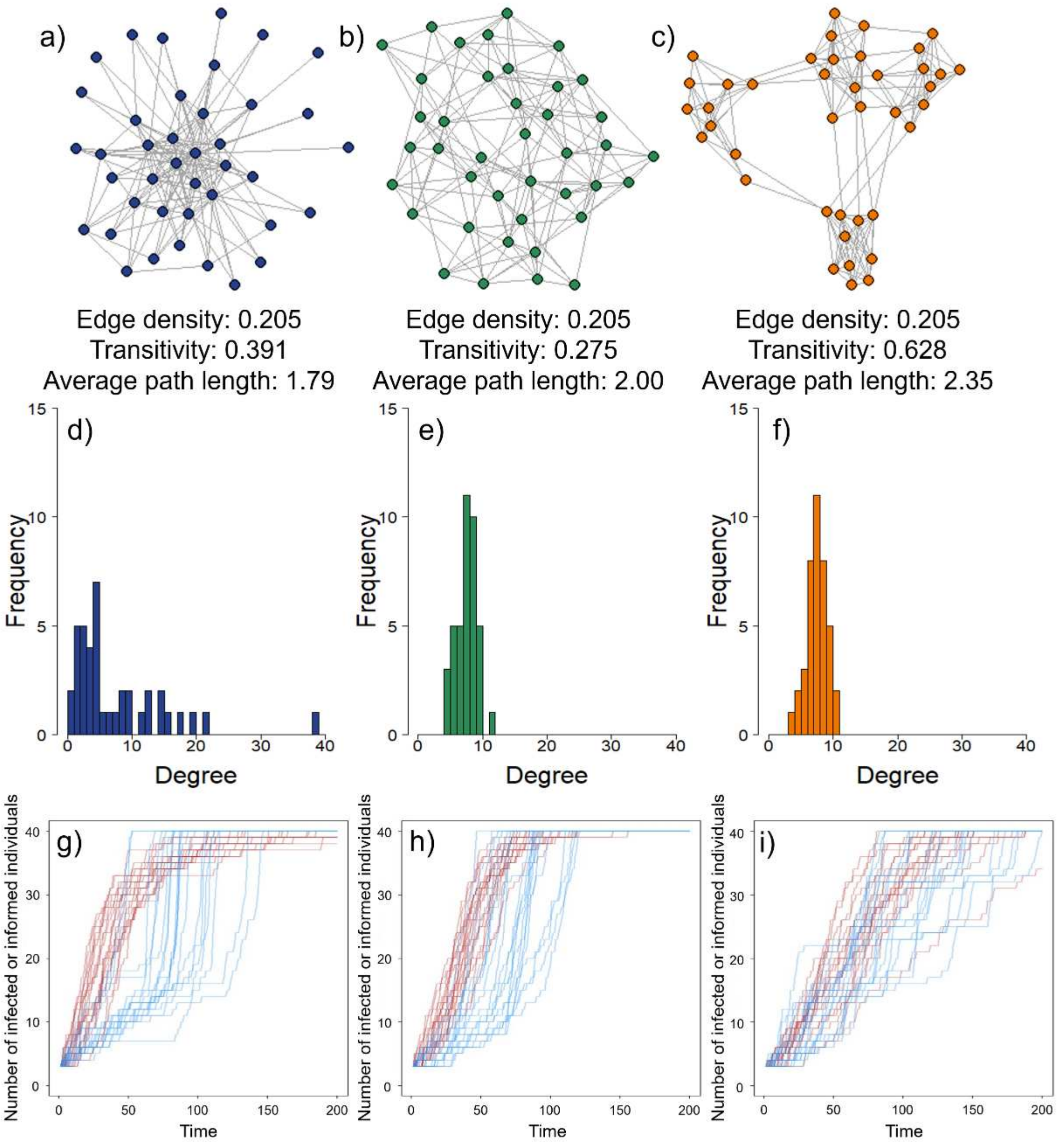


***Figure 2. Demonstration of three key types of network structure with important implications for transmission.*** *The network structure (a-c), degree distribution (d-f) and transmission dynamics (g-i) of a simple contagion model for infection (red) and conformist contagion model for information (blue) are illustrated. All networks plotted here have the same edge densities (proportion of potential edges that are connected). Scale-free (or approximately scale-free) networks (a,d,g) have highly heterogeneous degree distributions (i.e. high variation in connectivity) with some high-degree (very well connected) individuals acting as "hubs", causing average path lengths to be short and resulting in very rapid spread of parasites but slower spread of information. In small-world networks (b,e,h) most connections are to neighbours, but occasional long-range contacts act as "bridges", maintaining short average path lengths and enabling more rapid diffusion than random networks, and permitting faster spread via the cascade than the threshold model. In modular networks (c,f,i) most connections are to individuals in the same social community or module, resulting in high transitivity (or clustering of connections to 'friends of friends') and high average path lengths. Modular networks can have mixed effects on transmission speed that can depend on whether transmission follows a simple or conformist contagion dynamics. In this example, infection and information are able to spread at similar speeds through the modular network (i) but infection spreads more rapidly through scale-free (g) and small-world (h) network structures. Code for generating and plotting the networks and running the stochastic models is provided in the Supplementary Information.*

### *Heterogeneous degree distributions*

Many animal social networks have highly heterogeneous degree distributions, with certain highly connected individuals acting as "hubs". Taking these differences in connectivity into account is important to understand transmission dynamics. For parasite spread, models show that more heterogeneous degree distributions increase the speed of epidemic spread and result in a higher prevalence of epidemic peaks due to the presence of highly connected superspreader individuals (Barthélemy, et al. 2004, Lloyd-Smith, et al. 2005), but reduce the frequency of epidemics (Lloyd-Smith, et al. 2005). In more extreme situations where networks are truly scale-free, epidemics can spread almost instantaneously through populations (Barthélemy, et al. 2004), making them especially vulnerable to parasite spread. For information transmission, the role of degree heterogeneity is more complex. In some contexts, individuals occupying globally central roles in a network are more likely to acquire information (Aplin, et al. 2012, Jones, et al. 2017). However, when considering information transmission as complex contagion (as might be appropriate when individuals have conformity biases and accept information based on relative exposure), it is possible that individuals with many social connections might require stronger signals to distinguish a piece of information from the general "noise" received from their many associates (Hodas, et al. 2012, Hodas, et al. 2014). Conversely, lower-degree individuals may be more likely to utilise information sooner, as having a smaller number of ties means that fewer transmitting associates are required to achieve conformist transmission (González-Avella, et al. 2011). Differences in the nature of transmission between information (when considered to spread through complex contagion) and infection may generate differences in the "most susceptible" network position between the two types of transmission that will reduce the intensity of any trade-off between the acquisition of information and parasites.

Networks with highly heterogeneous degree distributions will allow the rapid spread of infection and (often) information through populations. However, we hypothesise that information will spread more slowly than infection through these types of network when conformist social learning strategies are used. Individuals with a larger number of connections will require a larger proportion number of their associates to transmit the information in order to achieve the same relative magnitude of exposure, compared to less centrally positioned individuals. Hubs may therefore be slower to respond to information than less well-connected individuals. This will drive differences in which network positions are most likely to acquire information and those which are most likely to become infected. Being highly connected may be disproportionately risky in terms of the risk of infection per unit of social information acquired (and used), while being embedded within a network region (i.e. sharing contacts with your associates) will minimise the risk of becoming infected per unit of social information gathered.

### *Small-world networks*

Small-world networks can arise as a result of the majority of social associations or interactions occurring mainly with close neighbours within groups, but with infrequent longer-range connections acting as "bridges" between regions of the network. It is easy to see how small-world properties might arise in animal networks through behaviours such as territoriality with occasional extra-territorial forays. For example, in African Lions *Panthera leo* contacts between prides are normally driven by space use, with prides from neighbouring territories coming into contact much more frequently. However, occasional contacts between prides that are normally spatially well-separated do occur, resulting in a network with small-world properties (Craft, et al. 2009). In small-world networks the epidemic threshold (i.e. the transmission probability at which epidemics become possible) decreases considerably as the likelihood of long-range connections in the network increases (Moore, et al. 2000). For example, in a territorial, monogamous animal this would equate to epidemics of a sexually-transmitted infection becoming more likely as extra-pair copulations occurred over greater distances rather than happening only among neighbouring territories.

As with models of parasite transmission, theoretical models predict that information flow will be faster in small-world networks than random networks (Alkemade, et al. 2005, de Kerchove, et al. 2009, Delre, et al. 2007, Nekovee, et al. 2007) and the importance of multiple social contacts in enabling transmission will be increased (de Kerchove, et al. 2009). The findings of de Kerchove, et al. (2009) suggest that to spread information effectively, an individual with long-range connections must have somewhat stable associations to "seed" individuals within the region of the network it is connected to, as a single interaction may be insufficient to enable transmission. If relative exposure to new information is important (i.e. it is necessary for a threshold proportion of contacts to be informed before an individual accepts information) then we can speculate that these "seed" individuals are more likely to be low-degree individuals who adopt information more rapidly due to their small number of other connections. The exception to this will occur if highly central individuals in the naïve group have a low information-use threshold (i.e. they require few demonstrators to transmit the information before adopting it themselves), which may be the case if individuals that acquire useful information tend to become more central in networks or if the bridging individuals are extremely influential due to their social status (or another trait).

Small-world networks are characterised by the importance of occasional long-range social connections involving small number of individuals. We suggest that the importance of these "bridge" individuals is easier to predict for parasite transmission, while for threshold models of information transmission their role will depend to a greater extent on the social learning rules of the individuals they are connected to, and therefore be more variable. We also predict that social dynamics will play a greater role in these small-world networks as the death of these "bridge" individuals or changes to their interactions will reduce the rate of global transmission of infection and information.

*Modular network structure*

Social networks with distinct social community structure are widespread in animals, especially in species living in stable social groups (Drewe, et al. 2009, Weber, et al. 2013, Weinrich 1991). Both community structure and transitivity (the tendency to be connected to 'friends of friends') reduce the size of parasite outbreaks but can lower the epidemic threshold. This makes it easier for less transmissible infections to spread, as the presence of many connections among the same set of individuals increases the probability of local spread, but these local connections reduce the probability of large-scale epidemics (Newman 2003, Sah, et al. 2017, Salathé, et al. 2010). The effect of modular structure is greater when interactions between individuals in different social communities are more infrequent so that sub-divisions between them are stronger (Sah, et al. 2017, Salathé, et al. 2010). A meta-analysis of animal social networks has shown that the impact of modularity on the spread of parasites is limited except when there are very few connections between communities (Sah, et al. 2017). The impact of modularity will also depend on the transmissibility of the parasite. For example, (Rozins, et al. 2018) demonstrated that the effect of the modular structure of empirically-derived European badger contact networks was greatest for simulated parasites with intermediate transmissibility (i.e. infectious enough to cause an outbreak but not so infectious that it can spread easily between social groups).

In contrast, models suggest that modularity may not interfere with information diffusion in the same way. In some scenarios a modular network structure may actually increase global diffusion by enhancing within-community spreading. For example, Nematzadeh, et al. (2014) used a threshold model to show that conformist social learning strategies could lead to information being transmitted most quickly in networks of intermediate modularity. The networks of species living in stable groups would therefore be expected to have reduced epidemic spreading, and potentially enhanced (or unchanged) information diffusion, as an outcome of being highly modular (Fig. 2). In this way, structural heterogeneity in animal social networks may mediate the trade-off between the transmission of information and infection, especially for group-living or fission-fusion social systems with more modular social networks.

We therefore suggest that a modular network structure may be critical in mediating the trade-off between minimising the spread of parasites and maximising the spread of information. Community structure can promote the spread of social information when individuals follow conformist social learning strategies, while trapping infection within particular regions of the network. We predict that the dual selection pressures imposed by the access to information and the risk of acquiring parasites will lead to natural selection generating modular network structures. The modularity of these structures will depend on the relative benefits information and costs of infection to individuals, and the social learning strategies that they use.

### *Different types of associations - Multilayer relationships*

As outlined in the previous section, different types of interaction will not all be equivalent for the transmission of infection or information. Considering how transmission dynamics vary for different types of interactions is therefore critical in understanding how animal societies might be adapted for efficient information transmission and minimal parasite spread. Multilayer networks allow multiple interaction types to be incorporated within a single conceptual framework (Kivelä, et al. 2014). A layer can denote different types of behavioural interaction between the same (or similar) set(s) of individuals, such as one layer for affiliative interactions and another for agonistic interactions (Finn, et al. 2019, Silk, et al. 2018b). Layers can also consist of interactions between different types of individuals, such as different sexes (Silk, et al. 2018c) or species (Silk, et al. 2018a), with edges between layers representing interactions between those types of individuals.

Theoretical models using multilayer networks have been valuable in understanding the spread of a single parasite species or piece of information through multiple types of interaction, and the consequences of multiple spreading processes occurring across the same set of individuals (for example, multiple information types: Liu et al. 2018a, multiple parasites: e.g. Azimi-Tafreshi 2016, or infection and information together: e.g. Funk et al. 2009; Granell, Gómez & Arenas 2013; Granell, Gómez & Arenas 2014; Guo et al. 2016, Funk, et al. 2010, Marceau, et al. 2011, Zhao, et al. 2014). Applying these approaches to animal behaviour research (Finn, et al. 2019, Silk, et al. 2018b) requires data on multiple types of social connections simultaneously (e.g. Franz, et al. 2015, Gazda, et al. 2015), and quantification of the importance of these different social connections for transmission (e.g. Aplin, et al. 2015).

Taking a multilayer approach also enables the integration of the indirect effect of positive and negative social relationships on transmission processes. Theoretical models on multilayer networks consider the effects of these different types of social relationships by modelling them as a type of transmission through the network, alongside infection and/or information. For example, one type of model considers the flow of social support that improves recovery rate from infection (which could, for example, represent the strength of affiliative relationships) on a second layer and has been used to show that social support can supress parasite outbreaks, but that the effect is dependent on network structure and the correlation between the layers (Chen, et al. 2018a, Chen, et al. 2018b). Using models such as these enables the impact of social buffering to be integrated into network models, to determine how it may shape the trade-off between encountering useful information and risking infection. At its simplest, if well-connected individuals are healthy and capable of resisting infection, then they do not face a trade-off at all.

Multiple spreading processes can also interact to promote or interfere with each other. For example, Liu, et al. (2018), when modelling the synergistic spread of multiple pieces of information transmitted simultaneously, showed that individuals having adopted one piece of information were subsequently more likely to adopt the other piece of information, one enhancing the other. A similar scenario in animal societies may be choosing to follow a particular individual’s migratory route leading to an increased likelihood of socially learning a more efficient version of that route (Berdahl, et al. 2018). Alternatively, different types of information might compete, with one piece of information overriding/displacing the other (Kostka, et al. 2008, Trpevski, et al. 2010). This could be important if the two pieces of information differ in their accuracy, or represent alternative strategies. Similarly, models suggest that multiple parasites spreading on a multilayer network can promote (Azimi-Tafreshi 2016) or inhibit (Funk, et al. 2010) each other's spread, and so are likely to be beneficial in understanding patterns of co-infection. When considering infection and information spread together, transmission models that integrate different transmission processes can provide fascinating insights (e.g. Funk, et al. 2009, Granell, et al. 2013, Granell, et al. 2014, Guo, et al. 2016). For example, Funk, et al. (2009) showed that information diffusing across a second network layer could slow epidemics, or even prevent the spread of infection across the first network layer, and that the impact of the information layer was amplified if it overlapped with the infection layer (i.e. had more similar patterns of interactions), or if the networks on each layer were highly clustered. These findings would suggest that if information about an infection can be spread through an animal social network via similar types of interaction as the infection itself, then infection avoidance behaviour can be much more effective in preventing the spread of parasites. Social insect colonies offer a perfect candidate system through combining the feasibility of experimental approaches, well documented roles for networks in information sharing (Preece, et al. 2014), and evidence for adaptive changes to network structure in response to infection (Stroeymeyt, et al. 2018).

We predict that animal social systems will have evolved such that different network structures for different types of interactions can help facilitate rapid acquisition of information while minimising the risk of infection. Multilayer network analysis may provide a valuable tool in modelling the combined spread of different parasites and/or different types of information. We expect that taking into account the full complexity of animal social systems using this approach will i) provide important new insights into transmission dynamics of both infection and parasites and ii) reveal crucial information as to when trade-offs between the gathering of information and avoidance of infection actually arise (and when they do not), and iii) be critical in revealing how this balance can be mediated.

# Social dynamics and the infection-information trade-off

### Temporal heterogeneity and transmission in animals

Most animal social networks are dynamic, varying predictably over time (Hirsch, et al. 2016) or across different contexts (Smith, et al. 2018). Accounting for these temporal changes can change how we understand transmission in animal social systems (e.g. Hirsch, et al. 2016, Springer, et al. 2017). If social associations change faster than transmission occurs, then considering contacts as dynamic is important when using models to understand transmission through a network (Taylor, et al. 2012, Volz, et al. 2007). While the presence of temporal changes to network structure in animals is well-established, very few empirical studies have considered temporal heterogeneity, or burstiness, in contact dynamics. “Bursty” contact dynamics consist of many contact events with a short gap between them, and occasional much longer gaps between contacts (Fig. 3), such as the clustering of heterospecific associations around a watering hole in an arid environment. “bursty” contact dynamics cause temporal clustering of interactions, which can impede the transmission of infection as compared to a scenario where contacts are distributed more uniformly through time, because such clustered repeated exposure can result in connections that redundant from a transmission perspective. In contrast, bursty contact dynamics may enhance the spread of information for some social learning strategies, as repeated exposures to novel information in quick succession might enhance learning opportunities by passing the information “acceptance threshold” (see Karsai, et al. 2011; Min, Goh & Kim 2013; c.f. Rocha, Liljeros & Holme 2011; Rocha & Blondel 2013). Consequently, varied temporal patterns of interactions could mitigate the potential trade-off between acquiring information and avoiding infection, especially for more “risky” interactions, such as between-group interactions in group-living species, which are more likely to be “bursty”. Temporally clustered interactions with new individuals will disproportionately increase the likelihood of acquiring information relative to becoming infected. Recent theoretical models have incorporated both temporal heterogeneity and structural heterogeneity (e.g. community structure), demonstrating that regulation of spread is typically dominated by one or the other (Delvenne, et al. 2015). This suggests that the importance of heterogeneous contact dynamics for transmission in animal societies may vary systematically with other aspects of the social system, such as the stability of social groups.

We recommend research that focuses on the implications of temporal clustering of interactions and/or contacts for the spread of information and parasites, providing valuable insights into how individuals balance the costs and benefits of their social interactions. We predict that “bursty” contact dynamics could enhance the transmission of some types of information (depending on the social learning strategies of individuals), while having no effect or even reducing the risk of parasite transmission – a good example may be lek mating systems. It would be possible to test these predictions in established experimental systems and then scale the findings to a population or network level using stochastic models. We also expect that accounting for the effects of heterogeneous contact dynamics will be most important for species living in highly fluid societies rather than more stable social groups.

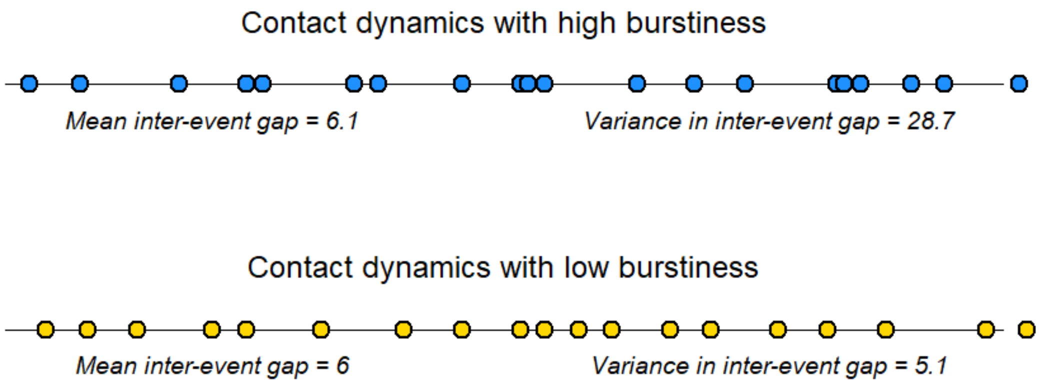


***Figure 3. An illustration of differences in the burstiness of contact dynamics****. When contact dynamics are “bursty”, there is a high variance in the gaps between contact events, resulting in clusters of contacts with occasional longer gaps. Bursty dynamics may promote the transmission of some types of information whilst reducing the risk of infection.*

**Responsive network dynamics and transmission in animals**

Animal social networks can change in response to the spread of infection (Croft, et al. 2011, Stroeymeyt, et al. 2018) and information (Kulahci, et al. 2018) with a key difference between infection and information being that changes to network structure during the spread of infection may be determined by the phenotype of both the hosts and their parasites (Franz, et al. 2018), while any changes to network structure in response to the acquisition of information are solely an outcome of selection on the "host", or "hosts" in the case of heterospecific transmission (Table 1). Theoretical models can provide some useful predictions as to how this affects transmission dynamics. Models where network connections can be altered in response to infection or information are referred to as adaptive network models (Bansal, et al. 2010, Funk, et al. 2015). The most common assumptions in infectious disease modelling are that individuals display infection-avoidance behaviour by either losing or reducing the strength of connections with infected individuals (e.g. Van Segbroeck, et al. 2010) or by replacing them with connections to other non-infected individuals (e.g. Shaw, et al. 2008). In the case of parasite spread, computational models indicate that adaptive networks typically have higher epidemic thresholds, delaying outbreaks and reducing peak prevalences (e.g. Gross, et al. 2006, Shaw, et al. 2008, Van Segbroeck, et al. 2010). These behavioural responses to infection also frequently impact aspects of the network structure, for example by increasing variation in the connectivity of susceptible individuals and causing infected individuals to be much more poorly connected (Shaw, et al. 2008) or by increasing community structure with community membership assorted by infection state (Yang, et al. 2012). While these changes reduce the impact of the current epidemic, they may make endemic disease more likely (Gross, et al. 2006, Shaw, et al. 2008) or even result in long-term epidemic re-emergence (Zhou, et al. 2012), which may have important implications for longer-term eco-evolutionary dynamics in animal populations. It is also possible for infection avoidance behaviour to exacerbate epidemics if individuals switch their connections from infected to susceptible individuals subsequent to being infected, although this remains relatively poorly explored (but see (Zhang, et al. 2012b)).

Many adaptive network models have previously assumed perfect knowledge about the infection status of other individuals, and this is unlikely to be the case in many natural host-parasite systems. Identifying when information is available about the infection status of individuals relative to when the infection is most transmissible (Stephenson, et al. 2018) will be crucial to understanding how “adaptive” changes to network structure can mediate the trade-off between information and parasite transmission. It may also be important to consider changes to the behaviour of infected individuals; sickness behaviour. Sickness behaviours in particular could be influenced by selection on hosts or parasites. At times, sickness behaviour could be favoured by both host and parasite (e.g. dispersal away from a highly related group; Iritani, et al. 2014), but at other times optimal outcomes may be directly opposed (e.g. reduction in number of contacts; Lopes, et al. 2016) and generate antagonistic co-evolution between the host and parasite.

The results from equivalent models of information transmission are more diverse. One model suggests that individuals may be more likely to cluster with those who are more inclined to use information they are deliberately transmitting (Jackson, et al. 2013), while another model suggests individuals will break ties with those who do not use the information they deliberately transmit (Zhang, et al. 2012a). In some species of animal, individuals may preferentially associate with those who will accept foraging information from them, so as to maximise the likelihood of gaining benefits from recruiting others to feed (Wright, et al. 2003). Similarly, a male displaying within a lek will attempt to maximise the number of individuals who receive their signals, while also choosing to give up and stop transmitting to those who are unlikely to mate with them (Patricelli, et al. 2009). In a similar manner to signalling individuals manipulating their physical environment (e.g. birds singing from prominent perches), individuals may also dynamically alter their social interactions so as to maximise their chances of transmitting information to less informed node (Liu, et al. 2014) if it is beneficial for them to do so (e.g. in highly related groups). In contrast to the avoidance behaviour expected in response to the spread of parasites, “adaptive” behaviours that favour the acquisition of useful information while minimising exposure to misinformation would be expected (Kulahci, et al. 2019), depending on previous interactions between the individuals involved. An individual who produces useful information may be more likely to have others use that information in the future, while an individual that frequently provides inaccurate information may be ignored (refractory behaviour). An important caveat to this idea is that an individual who has previously produced useful information may subsequently be more likely to cause misinformation to be transmitted (Modlmeier, et al. 2014), especially if the value of information changes over time (e.g. by becoming outdated). This can be exploited by individuals aiming to transmit misinformation to manipulate the receivers' behaviour to their advantage, as is the case in fork-tailed drongos (*Dicrurus adsimilis*) who mimic other species' alarm calls to steal food from meerkats (Flower, et al. 2014). Whether drongos flexibly change their social associations with heterospecifics once they have been identified as cheats by the local meerkat group remains to be determined.

Considering behavioural dynamics alongside transmission dynamics is important to our understanding of how individuals may resolve the conflict between the acquisition and transmission of information and infection. Obvious signs of infection or regular transmission of misinformation can result in individuals becoming less well connected in a network while transmission of useful information can lead to the opposite pattern. We predict that behavioural plasticity that causes patterns of social interactions to be modified in the presence of infection or innovations will therefore be a key mechanism by which this balance between the costs and benefits of being highly socially connected is mediated and expect that these behavioural dynamics are much more widespread than previously described. Behavioural dynamics are also likely to be closely interlinked with network structure, and we predict that behavioural responses to parasitism and information will co-vary with social structure (especially group dynamics and modularity) between populations.

# Future research priorities

Our review highlights several key priorities for future research. First, it is essential that we continue to build on our understanding of how infection and information are transmitted through natural populations. In particular, discovering how widespread the use of complex social learning strategies is in animals will be critical in revealing whether particular social network structures, and particular social network positions within them, favour the transfer or acquisition of information over and above that of parasites. Revealing the use of complex contagions or directed social learning strategies will require experimental approaches in study systems for which high-quality social network data are also available (e.g in primates: Carter, et al. 2016, or passerine birds: Farine, et al. 2015a). However, it would also be valuable to extend our understanding of social learning strategies away from these model systems to better quantify the generality of different forms of information spread. This could exploit experiments that test for learning being directed by traits such as social dominance (e.g. Benskin, et al. 2002, Jones, et al. 2016, Kendal, et al. 2015) or by conformity (e.g. Aplin, et al. 2015, Danchin, et al. 2018). In addition, we have emphasised how the transmission of information can also depend on different types of association or interaction than those influencing parasite transmission. A renewed effort to consider the consequences of the multilayer structure of animal social networks will be crucial to understanding differences in the opportunities for transmission of information and parasites within animal groups. Comparisons of the structure of interactions relevant for social learning, and those that provide opportunities for parasite transmission, are likely to be particularly informative.

We have also highlighted the importance of temporal heterogeneity in transmission-relevant contacts and the role of behavioural plasticity in response to parasite prevalence in mediating the trade-off between acquiring information and avoiding infection. Further research into social network dynamics will therefore also be critical in understanding how these two ecological processes shape the evolution of social network structure. Network dynamics that result from infection avoidance behaviour provide a context where both information and parasites are spreading, and the outcomes are inter-dependent. Therefore, work that builds on existing research addressing how social network structure responds to changes in parasite prevalence will be valuable (Stroeymeyt, et al. 2018), especially if it provides a mechanistic understanding of how individuals learn to change their behaviour (rapid spread of behavioural changes via conformist social learning, for example). Social insect colonies would be ideal for such experimental studies. These species lend themselves to high-throughput construction of replicated social networks, and studies quantifying the role of these networks in the transmission of information and parasites have already been conducted using such systems (Blonder, et al. 2011, Bos, et al. 2012, Stroeymeyt, et al. 2018). The final piece of this puzzle will be understanding changes in the behaviour of infected individuals (Lopes, et al. 2016) in a variety of different social systems and contexts, especially when social networks are kin-structured, given that the evolution of sickness behaviour is predicted to depend on population structure (Iritani, et al. 2014).

These experimental approaches will be most powerful when paired with novel mathematical models that examine the evolutionary ecology of individual social behaviour. Such models could demonstrate how social network positions are associated with different fitness outcomes when the costs and benefits provided by parasitism and social learning are varied. The theoretical transmission models described in this review, although extremely detailed, focus on the transmission processes themselves rather than placing them in a broader ecological and evolutionary context. Thus, combining these techniques for simulating transmission with evolutionary modelling will represent a key priority. In addition, tailoring theoretical network models to more accurately reflect typical contact behaviours of animals using recently established data repositories (Sah, et al. 2019) will help to provide more detailed predictions for different social systems. Combining theoretical and empirical work to develop data-based evolutionary models will be important to fully understand the implications of these differences in the transmission of infection and information for the evolution of animal social systems.

# Conclusions

Social network structure is fundamental to both the transmission of information and parasites through populations. Both represent important selection pressures on how individuals structure their social interactions. Individuals face a trade-off to maximise the acquisition of reliable information while minimising the risk of becoming infected with parasites. However, our understanding of this trade-off is complicated by how these processes depend on social network structure in different ways. The risk of acquiring infection typically increases monotonically with the frequency and duration of interaction with infectious individuals. In contrast, information acquisition is more complex, with the likelihood of accepting information often depending on exposure to that information in a non-linear fashion. For example, empirical evidence from some animal social networks suggests that acquisition of information might often be a threshold trait. A receiver's threshold of exposure could be determined by the proportion of associates demonstrating the behaviour, or could be determined more broadly by the identity, influence or traits of transmitters (e.g. social learning directed by dominance, familiarity, relatedness). Information transmission is also complicated by the sharing of both good and bad (or out-dated) information, and by "refractory" behaviours among recipients that result in the acquisition of information not affecting the behaviour of all individuals in the same way.

Crucially, these differences in the nature of transmission and the types of interactions that result in transmission can mediate the apparent trade-off between acquiring information and infection in social systems. Furthermore, plasticity of social behaviour can generate changes to social structures that can protect against the spread of parasites or promote the spread of information. In this way, behavioural plasticity is likely critical in regulating infection risk and information benefits obtained by social animals. Information transmission is often integral to behavioural responses to avoid infection, making quantifying differences in how information and infection are transmitted and their different routes of transmission even more important. Consequently, our understanding of the interplay between information and infection in shaping animal social systems requires a better grasp of how transmission is affected by the structural, temporal and multi-layered heterogeneities that are inherent to animal social networks.

# References

Alkemade, F. and Castaldi, C. 2005. Strategies for the Diffusion of Innovations on Social Networks. - Computational Economics 25: 3-23.

Allen, J., Weinrich, M., Hoppitt, W. and Rendell, L. 2013. Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales. - Science 340: 485-488.

Almberg, E. S., Cross, P. C., Dobson, A. P., Smith, D. W., Metz, M. C., Stahler, D. R. and Hudson, P. J. 2015. Social living mitigates the costs of a chronic illness in a cooperative carnivore. - Ecology letters 18: 660-667.

Anne, O. and Rasa, E. 1983. Dwarf mongoose and hornbill mutualism in the Taru Desert, Kenya. - Behavioral Ecology and Sociobiology 12: 181-190.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B. C. 2014. Experimentally induced innovations lead to persistent culture via conformity in wild birds. - Nature 518: 538.

Aplin, L. M., Farine, D. R., Morand-Ferron, J., Cockburn, A., Thornton, A. and Sheldon, B. C. 2015. Experimentally induced innovations lead to persistent culture via conformity in wild birds. - Nature 518: 538-541.

Aplin, L. M., Farine, D. R., Morand-Ferron, J. and Sheldon, B. C. 2012. Social networks predict patch discovery in a wild population of songbirds. - Proceedings of the Royal Society of London B: Biological Sciences 279 4199-4205.

Azimi-Tafreshi, N. 2016. Cooperative epidemics on multiplex networks. - Physical Review E 93: 042303.

Bakshy, E., Karrer, B. and Adamic, L. A. 2009. Social influence and the diffusion of user-created content. Proceedings of the 10th ACM conference on Electronic commerce. - ACM, pp. 325-334.

Balasubramaniam, K., Beisner, B., Vandeleest, J., Atwill, E. and McCowan, B. 2016. Social buffering and contact transmission: network connections have beneficial and detrimental effects on Shigella infection risk among captive rhesus macaques. - PeerJ 4: e2630.

Bansal, S., Read, J., Pourbohloul, B. and Meyers, L. A. 2010. The dynamic nature of contact networks in infectious disease epidemiology. - Journal of biological dynamics 4: 478-489.

Barthélemy, M., Barrat, A., Pastor-Satorras, R. and Vespignani, A. 2004. Velocity and hierarchical spread of epidemic outbreaks in scale-free networks. - Physical Review Letters 92: 178701.

Benskin, C. M. H., Mann, N. I., Lachlan, R. F. and Slater, P. J. B. 2002. Social learning directs feeding preferences in the zebra finch, Taeniopygia guttata. - Animal Behaviour 64: 823-828.

Berdahl, A. M., Kao, A. B., Flack, A., Westley, P. A. H., Codling, E. A., Couzin, I. D., Dell, A. I. and Biro, D. 2018. Collective animal navigation and migratory culture: from theoretical models to empirical evidence. - Philosophical Transactions of the Royal Society B: Biological Sciences 373: 20170009.

Berdoy, M., Webster, J. P. and Macdonald, D. W. 2000. Fatal attraction in rats infected with *Toxoplasma gondii*. - Proceedings of the Royal Society of London. Series B: Biological Sciences 267: 1591-1594.

Blanchet, S., Clobert, J. and Danchin, É. 2010. The role of public information in ecology and conservation: an emphasis on inadvertent social information. - Annals of the New York Academy of Sciences 1195: 149-168.

Blonder, B. and Dornhaus, A. 2011. Time-Ordered Networks Reveal Limitations to Information Flow in Ant Colonies. - PLOS ONE 6: e20298.

Blyton, M. D. J., Banks, S. C., Peakall, R., Lindenmayer, D. B. and Gordon, D. M. 2014. Not all types of host contacts are equal when it comes to E. coli transmission. - Ecology Letters 17: 970-978.

Boogert, N. J., Lachlan, R. F., Spencer, K. A., Templeton, C. N. and Farine, D. R. 2018. Stress hormones, social associations and song learning in zebra finches. - Philosophical Transactions of the Royal Society B: Biological Sciences 373: 20170290.

Boogert, N. J., Nightingale, G. F., Hoppitt, W. and Laland, K. N. 2014. Perching but not foraging networks predict the spread of novel foraging skills in starlings. - Behavioural processes 109: 135-144.

Bos, N., Lefèvre, T., Jensen, A. and d'Ettorre, P. 2012. Sick ants become unsociable. - Journal of evolutionary biology 25: 342-351.

Cantor, M. and Whitehead, H. 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. - Philosophical transactions of the Royal Society of London. Series B, Biological sciences 368: 20120340-20120340.

Carter, A. J., Tico, M. T. and Cowlishaw, G. 2016. Sequential phenotypic constraints on social information use in wild baboons. - Elife 5: e13125.

Centola, D. 2010. The Spread of Behavior in an Online Social Network Experiment. - Science 329: 1194-1197.

Chen, X., Wang, R., Tang, M., Cai, S., Stanley, H. E. and Braunstein, L. A. 2018a. Suppressing epidemic spreading in multiplex networks with social-support. - New Journal of Physics 20: 013007.

Chen, X., Wang, W., Cai, S., Stanley, H. E. and Braunstein, L. A. 2018b. Optimal resource diffusion for suppressing disease spreading in multiplex networks. - Journal of Statistical Mechanics: Theory and Experiment 2018: 053501.

Coelho, C. G., Falótico, T., Izar, P., Mannu, M., Resende, B. D., Siqueira, J. O. and Ottoni, E. B. 2015. Social learning strategies for nut-cracking by tufted capuchin monkeys (Sapajus spp.). - Animal Cognition 18: 911-919.

Coolen, I., Bergen, Y. V., Day, R. L. and Laland, K. N. 2003. Species difference in adaptive use of public information in sticklebacks. - Proceedings of the Royal Society of London. Series B: Biological Sciences 270: 2413-2419.

Coussi-Korbel, S. and Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. - Animal behaviour 50: 1441-1453.

Craft, M. E. 2015. Infectious disease transmission and contact networks in wildlife and livestock. - Philosophical Transactions of the Royal Society B: Biological Sciences 370: 20140107.

Craft, M. E., Volz, E., Packer, C. and Meyers, L. A. 2009. Distinguishing epidemic waves from disease spillover in a wildlife population. - Proceedings of the Royal Society of London B: Biological Sciences: rspb. 2008.1636.

Croft, D. P., Edenbrow, M., Darden, S. K., Ramnarine, I. W., van Oosterhout, C. and Cable, J. 2011. Effect of gyrodactylid ectoparasites on host behaviour and social network structure in guppies Poecilia reticulata. - Behavioral Ecology and Sociobiology 65: 2219-2227.

Dall, S. R., Giraldeau, L.-A., Olsson, O., McNamara, J. M. and Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. - Trends in ecology & evolution 20: 187-193.

Danchin, E., Giraldeau, L.-A., Valone, T. J. and Wagner, R. H. 2004. Public information: from nosy neighbors to cultural evolution. - Science 305: 487-491.

Danchin, E., Nöbel, S., Pocheville, A., Dagaeff, A.-C., Demay, L., Alphand, M., Ranty-Roby, S., van Renssen, L., Monier, M., Gazagne, E., Allain, M. and Isabel, G. 2018. Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions. - Science 362: 1025-1030.

Daszak, P., Cunningham, A. A. and Hyatt, A. D. 2000. Emerging Infectious Diseases of Wildlife-- Threats to Biodiversity and Human Health. - Science 287: 443-449.

Dawson, E. H. and Chittka, L. 2012. Conspecific and heterospecific information use in bumblebees. - PloS one 7: e31444-e31444.

de Kerchove, C., Krings, G., Lambiotte, R., Van Dooren, P. and Blondel, V. D. 2009. Role of second trials in cascades of information over networks. - Physical Review E 79: 016114.

Delahay, R. J., Cheeseman, C. L. and Clifton-Hadley, R. S. 2001. Wildlife disease reservoirs: the epidemiology of Mycobacterium bovis infection in the European badger (Meles meles) and other British mammals. - Tuberculosis 81: 43-49.

Delre, S. A., Jager, W. and Janssen, M. A. 2007. Diffusion dynamics in small-world networks with heterogeneous consumers. - Computational and Mathematical Organization Theory 13: 185-202.

Delvenne, J.-C., Lambiotte, R. and Rocha, L. E. 2015. Diffusion on networked systems is a question of time or structure. - Nature communications 6: 7366.

Drewe, J., Madden, J. and Pearce, G. 2009. The social network structure of a wild meerkat population: 1. Inter-group interactions. - Behavioral Ecology and Sociobiology 63: 1295-1306.

Evans, J. C., Jones, T. B. and Morand-Ferron, J. 2018. Dominance and the initiation of group feeding events: the modifying effect of sociality. - Behavioral Ecology 29: 448-458.

Ezenwa, V. O., Archie, E. A., Craft, M. E., Hawley, D. M., Martin, L. B., Moore, J. and White, L. 2016a. Host behaviour and parasite feedback: an essential link between animal behaviour and disease ecology. - Proceedings of the Royal Society B: Biological Sciences 283: 20153078.

Ezenwa, V. O., Ghai, R. R., McKay, A. F. and Williams, A. E. 2016b. Group living and pathogen infection revisited. - Current Opinion in Behavioral Sciences 12: 66-72.

Ezenwa, V. O. and Worsley-Tonks, K. E. 2018. Social living simultaneously increases infection risk and decreases the cost of infection. - Proceedings of the Royal Society B 285: 20182142.

Farine, D. R., Aplin, L. M., Sheldon, B. C. and Hoppitt, W. 2015a. Interspecific social networks promote information transmission in wild songbirds. - Proceedings of the Royal Society B: Biological Sciences 282: 20142804.

Farine, Damien R., Spencer, Karen A. and Boogert, Neeltje J. 2015b. Early-Life Stress Triggers Juvenile Zebra Finches to Switch Social Learning Strategies. - Current Biology 25: 2184-2188.

Faust, C. L., McCallum, H. I., Bloomfield, L. S. P., Gottdenker, N. L., Gillespie, T. R., Torney, C. J., Dobson, A. P. and Plowright, R. K. 2018. Pathogen spillover during land conversion. - Ecology Letters 21: 471-483.

Ferrari, M. C. O. and Chivers, D. P. 2008. Cultural learning of predator recognition in mixed-species assemblages of frogs: the effect of tutor-to-observer ratio. - Animal Behaviour 75: 1921-1925.

Finn, K. R., Silk, M. J., Porter, M. A. and Pinter-Wollman, N. 2019. The use of multilayer network analysis in animal behaviour. - Animal Behaviour 149: 7-22.

Firth, J. A. 2020. Considering Complexity: Animal Social Networks and Behavioural Contagions. - Trends in Ecology & Evolution 35: 100-104.

Flower, T. P., Gribble, M. and Ridley, A. R. 2014. Deception by Flexible Alarm Mimicry in an African Bird. - Science 344: 513-516.

Franz, M., Altmann, J. and Alberts, S. C. 2015. Knockouts of high-ranking males have limited impact on baboon social networks. - Current Zoology 61: 107-113.

Franz, M., Kramer-Schadt, S., Greenwood, A. D. and Courtiol, A. 2018. Sickness-induced lethargy can increase host contact rates and pathogen spread in water-limited landscapes. - Functional ecology 32: 2194-2204.

Funk, S., Bansal, S., Bauch, C. T., Eames, K. T., Edmunds, W. J., Galvani, A. P. and Klepac, P. 2015. Nine challenges in incorporating the dynamics of behaviour in infectious diseases models. - Epidemics 10: 21-25.

Funk, S., Gilad, E., Watkins, C. and Jansen, V. A. 2009. The spread of awareness and its impact on epidemic outbreaks. - Proceedings of the National Academy of Sciences 106: 6872-6877.

Funk, S. and Jansen, V. A. 2010. Interacting epidemics on overlay networks. - Physical Review E 81: 036118.

Gazda, S., Iyer, S., Killingback, T., Connor, R. and Brault, S. 2015. The importance of delineating networks by activity type in bottlenose dolphins (Tursiops truncatus) in Cedar Key, Florida. - Royal Society open science 2: 140263.

Giraldeau, L. A., Valone, T. J. and Templeton, J. J. 2002. Potential disadvantages of using socially acquired information. - Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 357: 1559-1566.

Godfrey, S. S. 2013. Networks and the ecology of parasite transmission: A framework for wildlife parasitology. - International Journal for Parasitology: Parasites and Wildlife 2: 235-245.

Godfrey, S. S., Bull, C. M., James, R. and Murray, K. 2009. Network structure and parasite transmission in a group living lizard, the gidgee skink, Egernia stokesii. - Behavioral Ecology and Sociobiology 63: 1045-1056.

González-Avella, J. C., Eguíluz, V. M., Marsili, M., Vega-Redondo, F. and San Miguel, M. 2011. Threshold Learning Dynamics in Social Networks. - PLOS ONE 6: e20207.

Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C. and Ruxton, G. D. 2010. Interspecific information transfer influences animal community structure. - Trends in Ecology & Evolution 25: 354-361.

Goodale, E. and Kotagama, S. W. 2008. Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. - Behavioral Ecology 19: 887-894.

Gosling, L. M. and Roberts, S. C. 2001. Scent-marking by male mammals: cheat-proof signals to competitors and mates. Advances in the Study of Behavior. Elsevier, pp. 169-217.

Granell, C., Gómez, S. and Arenas, A. 2013. Dynamical interplay between awareness and epidemic spreading in multiplex networks. - Physical review letters 111: 128701.

Granell, C., Gómez, S. and Arenas, A. 2014. Competing spreading processes on multiplex networks: awareness and epidemics. - Physical review E 90: 012808.

Griffin, R. H. and Nunn, C. L. 2012. Community structure and the spread of infectious disease in primate social networks. - Evolutionary Ecology 26: 779-800.

Gross, T., D'Lima, C. J. D. and Blasius, B. 2006. Epidemic dynamics on an adaptive network. - Physical review letters 96: 208701.

Guo, Q., Lei, Y., Jiang, X., Ma, Y., Huo, G. and Zheng, Z. 2016. Epidemic spreading with activity-driven awareness diffusion on multiplex network. - Chaos: An Interdisciplinary Journal of Nonlinear Science 26: 043110.

Gurley, N. and Johnson, D. K. 2016. Viral economics: an epidemiological model of knowledge diffusion in economics. - Oxford Economic Papers 69: 320-331.

Hamilton, D. G., Jones, M. E., Cameron, E. Z., McCallum, H., Storfer, A., Hohenlohe, P. A. and Hamede, R. K. 2019. Rate of intersexual interactions affects injury likelihood in Tasmanian devil contact networks. - Behavioral Ecology 30: 1087-1095.

Haun, Daniel B. M., Rekers, Y. and Tomasello, M. 2012. Majority-Biased Transmission in Chimpanzees and Human Children, but Not Orangutans. - Current Biology 22: 727-731.

Hirsch, B. T., Reynolds, J. J. H., Gehrt, S. D. and Craft, M. E. 2016. Which mechanisms drive seasonal rabies outbreaks in raccoons? A test using dynamic social network models. - Journal of Applied Ecology 53: 804-813.

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W. and Gruber, T. 2014. Social Network Analysis Shows Direct Evidence for Social Transmission of Tool Use in Wild Chimpanzees. - PLOS Biology 12: e1001960.

Hodas, N. O. and Lerman, K. 2012. How visibility and divided attention constrain social contagion. Privacy, Security, Risk and Trust (PASSAT), 2012 International Conference on and 2012 International Confernece on Social Computing (SocialCom). - IEEE, pp. 249-257.

Hodas, N. O. and Lerman, K. 2014. The Simple Rules of Social Contagion. - Scientific Reports 4: 4343.

Hollen, L. I. and Radford, A. N. 2009. The development of alarm call behaviour in mammals and birds. - Animal Behaviour 78: 791-800.

Hoyt, J. R., Langwig, K. E., White, J. P., Kaarakka, H. M., Redell, J. A., Kurta, A., DePue, J. E., Scullon, W. H., Parise, K. L., Foster, J. T., Frick, W. F. and Kilpatrick, A. M. 2018. Cryptic connections illuminate pathogen transmission within community networks. - Nature 563: 710-713.

Iritani, R. and Iwasa, Y. 2014. Parasite infection drives the evolution of state-dependent dispersal of the host. - Theoretical Population Biology 92: 1-13.

Jackson, M. O. and López-Pintado, D. 2013. Diffusion and contagion in networks with heterogeneous agents and homophily. - Network Science 1: 49-67.

Jones, C. E. and Monfils, M.-H. 2016. Dominance status predicts social fear transmission in laboratory rats. - Animal Cognition 19: 1051-1069.

Jones, T. B., Aplin, L. M., Devost, I. and Morand-Ferron, J. 2017. Individual and ecological determinants of social information transmission in the wild. - Animal Behaviour 129: 93-101.

Juher, D., Kiss, I. Z. and Saldaña, J. 2015. Analysis of an epidemic model with awareness decay on regular random networks. - Journal of theoretical biology 365: 457-468.

Karsai, M., Kivelä, M., Pan, R. K., Kaski, K., Kertész, J., Barabási, A.-L. and Saramäki, J. 2011. Small but slow world: How network topology and burstiness slow down spreading. - Physical Review E 83: 025102.

Kavaliers, M., Colwell, D. D. and Choleris, E. 2005. Kinship, familiarity and social status modulate social learning about "micropredators"(biting flies) in deer mice. - Behavioral Ecology and Sociobiology 58: 60-71.

Kempe, D., Kleinberg, J. and Tardos, É. 2003. Maximizing the spread of influence through a social network. Proceedings of the ninth ACM SIGKDD international conference on Knowledge discovery and data mining. - ACM, pp. 137-146.

Kendal, R., Hopper, L. M., Whiten, A., Brosnan, S. F., Lambeth, S. P., Schapiro, S. J. and Hoppitt, W. 2015. Chimpanzees copy dominant and knowledgeable individuals: implications for cultural diversity. - Evolution and Human Behavior 36: 65-72.

Kendal, R. L., Custance, D. M., Kendal, J. R., Vale, G., Stoinski, T. S., Rakotomalala, N. L. and Rasamimanana, H. 2010. Evidence for social learning in wild lemurs (Lemur catta). - Learning & Behavior 38: 220-234.

Kivelä, M., Arenas, A., Barthelemy, M., Gleeson, J. P., Moreno, Y. and Porter, M. A. 2014. Multilayer networks. - Journal of complex networks 2: 203-271.

Klein, B. A., Vogt, M., Unrein, K. and Reineke, D. M. 2018. Followers of honey bee waggle dancers change their behaviour when dancers are sleep-restricted or perform imprecise dances. - Animal Behaviour 146: 71-77.

Koops, M. A. 2004. Reliability and the value of information. - Animal Behaviour 67: 103-111.

Kostka, J., Oswald, Y. A. and Wattenhofer, R. 2008. Word of mouth: Rumor dissemination in social networks. International Colloquium on Structural Information and Communication Complexity. - Springer, pp. 185-196.

Krause, J., Ruxton, G. D., Ruxton, G. D. and Ruxton, I. G. 2002. Living in groups. - Oxford University Press.

Kreuder Johnson, C., Hitchens, P. L., Smiley Evans, T., Goldstein, T., Thomas, K., Clements, A., Joly, D. O., Wolfe, N. D., Daszak, P., Karesh, W. B. and Mazet, J. K. 2015. Spillover and pandemic properties of zoonotic viruses with high host plasticity. - Scientific Reports 5: 14830.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. and Sherwin, W. B. 2005. Cultural transmission of tool use in bottlenose dolphins. - Proceedings of the National Academy of Sciences 102: 8939-8943.

Kulahci, I. G., Ghazanfar, A. A. and Rubenstein, D. I. 2018. Knowledgeable Lemurs Become More Central in Social Networks. - Current Biology 28: 1306-1310.e2.

Kulahci, I. G. and Quinn, J. L. 2019. Dynamic Relationships between Information Transmission and Social Connections. - Trends in ecology & evolution.

Laland, K. N. 2004. Social learning strategies. - Animal Learning & Behavior 32: 4-14.

Laland, K. N. and Williams, K. 1998. Social transmission of maladaptive information in the guppy. - Behavioral Ecology 9: 493-499.

Lilly, M. V., Lucore, E. C. and Tarvin, K. A. 2019. Eavesdropping grey squirrels infer safety from bird chatter. - PloS one 14.

Liu, C. and Zhang, Z.-K. 2014. Information spreading on dynamic social networks. - Communications in Nonlinear Science and Numerical Simulation 19: 896-904.

Liu, Q.-H., Wang, W., Cai, S.-M., Tang, M. and Lai, Y.-C. 2018. Synergistic interactions promote behavior spreading and alter phase transitions on multiplex networks. - Physical Review E 97: 022311.

Lloyd-Smith, J. O., Schreiber, S. J., Kopp, P. E. and Getz, W. M. 2005. Superspreading and the effect of individual variation on disease emergence. - Nature 438: 355.

Longdon, B., Hadfield, J. D., Webster, C. L., Obbard, D. J. and Jiggins, F. M. 2011. Host phylogeny determines viral persistence and replication in novel hosts. - PLoS pathogens 7: e1002260-e1002260.

Loot, G., Brosse, S., Lek, S. and Guégan, J.-F. 2001. Behaviour of roach (Rutilus rutilus L.) altered by Ligula intestinalis (Cestoda: Pseudophyllidea): a field demonstration. - Freshwater Biology 46: 1219-1227.

Lopes, P. C., Block, P. and König, B. 2016. Infection-induced behavioural changes reduce connectivity and the potential for disease spread in wild mice contact networks. - Scientific Reports 6: 31790.

Lusseau, D. 2003. The emergent properties of a dolphin social network. - Proceedings of the Royal Society of London B: Biological Sciences 270: S186-S188.

Lusseau, D. and Newman, M. E. J. 2004. Identifying the role that animals play in their social networks. - Proceedings of the Royal Society of London. Series B: Biological Sciences 271: S477-S481.

Macy, M. W. 1991. Chains of cooperation: Threshold effects in collective action. - American Sociological Review: 730-747.

Magrath, Robert D., Haff, Tonya M., McLachlan, Jessica R. and Igic, B. 2015. Wild Birds Learn to Eavesdrop on Heterospecific Alarm Calls. - Current Biology 25: 2047-2050.

Mann, J., Stanton, M. A., Patterson, E. M., Bienenstock, E. J. and Singh, L. O. 2012. Social networks reveal cultural behaviour in tool-using dolphins. - Nature communications 3: 980.

Marceau, V., Noël, P.-A., Hébert-Dufresne, L., Allard, A. and Dubé, L. J. 2011. Modeling the dynamical interaction between epidemics on overlay networks. - Physical Review E 84: 026105.

McComb, K., Moss, C., Durant, S. M., Baker, L. and Sayialel, S. 2001. Matriarchs as repositories of social knowledge in african elephants. - Science 292: 491-494.

Min, B., Goh, K.-I. and Kim, I.-M. 2013. Suppression of epidemic outbreaks with heavy-tailed contact dynamics. - EPL (Europhysics Letters) 103: 50002.

Modlmeier, A. P., Keiser, C. N., Watters, J. V., Sih, A. and Pruitt, J. N. 2014. The keystone individual concept: an ecological and evolutionary overview. - Animal Behaviour 89: 53-62.

Moore, C. and Newman, M. E. 2000. Epidemics and percolation in small-world networks. - Physical Review E 61: 5678.

Morgan, T. J. H. and Laland, K. N. 2012. The biological bases of conformity. - Frontiers in neuroscience 6: 87-87.

Nekovee, M., Moreno, Y., Bianconi, G. and Marsili, M. 2007. Theory of rumour spreading in complex social networks. - Physica A: Statistical Mechanics and its Applications 374: 457-470.

Nematzadeh, A., Ferrara, E., Flammini, A. and Ahn, Y.-Y. 2014. Optimal Network Modularity for Information Diffusion. - Physical Review Letters 113: 088701.

Newman, M. E. 2002. Spread of epidemic disease on networks. - Physical review E 66: 016128.

Newman, M. E. 2003. Properties of highly clustered networks. - Physical Review E 68: 026121.

Nöbel, S., Allain, M., Isabel, G. and Danchin, E. 2018. Mate copying in Drosophila melanogaster males. - Animal Behaviour 141: 9-15.

Nocera, J. J., Forbes, G. J. and Giraldeau, L.-A. 2005. Inadvertent social information in breeding site selection of natal dispersing birds. - Proceedings of the Royal Society B: Biological Sciences 273: 349-355.

Patricelli, G. L. and Krakauer, A. H. 2009. Tactical allocation of effort among multiple signals in sage grouse: an experiment with a robotic female. - Behavioral Ecology 21: 97-106.

Pelletier, F., Garant, D. and Hendry, A. P. 2009. Eco-evolutionary dynamics. - Philosophical Transactions of the Royal Society B: Biological Sciences 364: 1483-1489.

Plowright, R. K., Parrish, C. R., McCallum, H., Hudson, P. J., Ko, A. I., Graham, A. L. and Lloyd-Smith, J. O. 2017. Pathways to zoonotic spillover. - Nature Reviews Microbiology 15: 502-510.

Preece, K. and Beekman, M. 2014. Honeybee waggle dance error: adaption or constraint? Unravelling the complex dance language of honeybees. - Animal Behaviour 94: 19-26.

Radford, A. N. 2004. Vocal Coordination of Group Movement by Green Woodhoopoes (*Phoeniculus purpureus*). - Ethology 110: 11-20.

Randall, D. A., Marino, J., Haydon, D. T., Sillero-Zubiri, C., Knobel, D. L., Tallents, L. A., Macdonald, D. W. and Laurenson, M. K. 2006. An integrated disease management strategy for the control of rabies in Ethiopian wolves. - Biological Conservation 131: 151-162.

Rieucau, G. and Giraldeau, L.-A. 2011. Exploring the costs and benefits of social information use: an appraisal of current experimental evidence. - Philosophical Transactions of the Royal Society B: Biological Sciences 366: 949-957.

Rocha, L. E. and Blondel, V. D. 2013. Bursts of vertex activation and epidemics in evolving networks. - PLoS computational biology 9: e1002974.

Rocha, L. E., Liljeros, F. and Holme, P. 2011. Simulated epidemics in an empirical spatiotemporal network of 50,185 sexual contacts. - PLoS computational biology 7: e1001109.

Romano, V., Sueur, C. and MacIntosh, A. J. 2020. The trade-off between information and pathogen transmission in animal societies. -.

Rozins, C., Silk, M. J., Croft, D. P., Delahay, R. J., Hodgson, D. J., McDonald, R. A., Weber, N. and Boots, M. 2018. Social structure contains epidemics and regulates individual roles in disease transmission in a group-living mammal. - Ecology and Evolution 8: 12044-12055.

Sah, P., Leu, S. T., Cross, P. C., Hudson, P. J. and Bansal, S. 2017. Unraveling the disease consequences and mechanisms of modular structure in animal social networks. - Proceedings of the National Academy of Sciences: 201613616.

Sah, P., Méndez, J. D. and Bansal, S. 2019. A multi-species repository of social networks. - Scientific Data 6: 44.

Salathé, M. and Jones, J. H. 2010. Dynamics and control of diseases in networks with community structure. - PLoS computational biology 6: e1000736.

Sapolsky, R. M. 2005. The Influence of Social Hierarchy on Primate Health. - Science 308: 648-652.

Schakner, Z. A., Petelle, M. B., Tennis, M. J., Leeuw, B. K. V. d., Stansell, R. T. and Blumstein, D. T. 2017. Social associations between California sea lions influence the use of a novel foraging ground. - Royal Society Open Science 4: 160820.

Scharf, I., Modlmeier, A. P., Beros, S. and Foitzik, S. 2012. Ant societies buffer individual-level effects of parasite infections. - The American Naturalist 180: 671-683.

Schmidt, K. A., Dall, S. R. X. and Van Gils, J. A. 2010. The ecology of information: an overview on the ecological significance of making informed decisions. - Oikos 119: 304-316.

Seppänen, J.-T., Forsman, J. T., Mönkkönen, M. and Thomson, R. L. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. - Ecology 88: 1622-1633.

Shaw, L. B. and Schwartz, I. B. 2008. Fluctuating epidemics on adaptive networks. - Physical Review E 77: 066101.

Shizuka, D. and Johnson, A. E. 2019. How demographic processes shape animal social networks. - Behavioral Ecology.

Silk, M. J., Croft, D. P., Delahay, R. J., Hodgson, D. J., Boots, M., Weber, N. and McDonald, R. A. 2017a. Using Social Network Measures in Wildlife Disease Ecology, Epidemiology, and Management. - BioScience 67: 245-257.

Silk, M. J., Croft, D. P., Delahay, R. J., Hodgson, D. J., Weber, N., Boots, M. and McDonald, R. A. 2017b. The application of statistical network models in disease research. - Methods in Ecology and Evolution 8: 1026-1041.

Silk, M. J., Drewe, J. A., Delahay, R. J., Weber, N., Steward, L. C., Wilson-Aggarwal, J., Boots, M., Hodgson, D. J., Croft, D. P. and McDonald, R. A. 2018a. Quantifying direct and indirect contacts for the potential transmission of infection between species using a multilayer contact network. - Behaviour 155: 731-757.

Silk, M. J., Finn, K. R., Porter, M. A. and Pinter-Wollman, N. 2018b. Can Multilayer Networks Advance Animal Behavior Research? - Trends in Ecology & Evolution 33: 376-378.

Silk, M. J., Weber, N. L., Steward, L. C., Hodgson, D. J., Boots, M., Croft, D. P., Delahay, R. J. and McDonald, R. A. 2018c. Contact networks structured by sex underpin sex-specific epidemiology of infection. - Ecology Letters 21: 309-318.

Smith, J. E., Gamboa, D. A., Spencer, J. M., Travenick, S. J., Ortiz, C. A., Hunter, R. D. and Sih, A. 2018. Split between two worlds: automated sensing reveals links between above- and belowground social networks in a free-living mammal. - Philosophical Transactions of the Royal Society B: Biological Sciences 373: 20170249.

Springer, A., Kappeler, P. M. and Nunn, C. L. 2017. Dynamic vs. static social networks in models of parasite transmission: predicting Cryptosporidium spread in wild lemurs. - Journal of Animal Ecology 86: 419-433.

St Clair, J. J. H., Burns, Z. T., Bettaney, E. M., Morrissey, M. B., Otis, B., Ryder, T. B., Fleischer, R. C., James, R. and Rutz, C. 2015. Experimental resource pulses influence social-network dynamics and the potential for information flow in tool-using crows. - Nature Communications 6: 7197.

Stattner, E. and Vidot, N. 2011. Social network analysis in epidemiology: Current trends and perspectives. 2011 Fifth International Conference on Research Challenges in Information Science. - IEEE, pp. 1-11.

Stephenson, J. F., Perkins, S. E. and Cable, J. 2018. Transmission risk predicts avoidance of infected conspecifics in Trinidadian guppies. - Journal of Animal Ecology 87: 1525-1533.

Stroeymeyt, N., Grasse, A. V., Crespi, A., Mersch, D. P., Cremer, S. and Keller, L. 2018. Social network plasticity decreases disease transmission in a eusocial insect. - Science 362: 941-945.

Swaney, W., Kendal, J., Capon, H., Brown, C. and Laland, K. N. 2001. Familiarity facilitates social learning of foraging behaviour in the guppy. - Animal Behaviour 62: 591-598.

Taylor, M., Taylor, T. J. and Kiss, I. Z. 2012. Epidemic threshold and control in a dynamic network. - Physical Review E 85: 016103.

Templeton, C. N. and Greene, E. 2007. Nuthatches eavesdrop on variations in heterospecific chickadee mobbing alarm calls. - Proceedings of the National Academy of Sciences 104: 5479-5482.

Toth, Z. and Griggio, M. 2011. Leaders are more attractive: birds with bigger yellow breast patches are followed by more group-mates in foraging groups. - PloS one 6: e26605.

Tóth, Z., Tuliozi, B., Baldan, D., Hoi, H. and Griggio, M. 2017. The effect of social connections on the discovery of multiple hidden food patches in a bird species. - Scientific Reports 7: 816.

Trpevski, D., Tang, W. K. S. and Kocarev, L. 2010. Model for rumor spreading over networks. - Physical Review E 81: 056102.

Tunc, I. and Shaw, L. B. 2014. Effects of community structure on epidemic spread in an adaptive network. - Physical Review E 90: 022801.

Valsecchi, P., Choleris, E., Moles, A., Guo, C. and Mainardi, M. 1996. Kinship and familiarity as factors affecting social transfer of food preferences in adult Mongolian gerbils (Meriones unguiculatus). - Journal of Comparative Psychology 110: 243.

Van Segbroeck, S., Santos, F. C. and Pacheco, J. M. 2010. Adaptive contact networks change effective disease infectiousness and dynamics. - PLoS computational biology 6: e1000895.

VanderWaal, K. L., Atwill, E. R., Isbell, L. A. and McCowan, B. 2014. Linking social and pathogen transmission networks using microbial genetics in giraffe (Giraffa camelopardalis). - Journal of Animal Ecology 83: 406-414.

VanderWaal, K. L. and Ezenwa, V. O. 2016. Heterogeneity in pathogen transmission: mechanisms and methodology. - Functional Ecology 30: 1606-1622.

Viana, M., Mancy, R., Biek, R., Cleaveland, S., Cross, P. C., Lloyd-Smith, J. O. and Haydon, D. T. 2014. Assembling evidence for identifying reservoirs of infection. - Trends in Ecology & Evolution 29: 270-279.

Volz, E. 2008. SIR dynamics in random networks with heterogeneous connectivity. - Journal of mathematical biology 56: 293-310.

Volz, E. and Meyers, L. A. 2007. Susceptible–infected–recovered epidemics in dynamic contact networks. - Proceedings of the Royal Society of London B: Biological Sciences 274: 2925-2934.

Von Frisch, K. 1967. The dance language and orientation of bees. -.

Walker, T. N. and Hughes, W. O. 2009. Adaptive social immunity in leaf-cutting ants. - Biology Letters: rsbl20090107.

Wang, L. and Wood, B. C. 2011. An epidemiological approach to model the viral propagation of memes. - Applied Mathematical Modelling 35: 5442-5447.

Ward, A. J., Sumpter, D. J., Couzin, I. D., Hart, P. J. and Krause, J. 2008. Quorum decision-making facilitates information transfer in fish shoals. - Proceedings of the National Academy of Sciences 105: 6948-6953.

Weber, N., Carter, S. P., Dall, S. R. X., Delahay, R. J., McDonald, J. L., Bearhop, S. and McDonald, R. A. 2013. Badger social networks correlate with tuberculosis infection. - Current Biology 23: R915-R916.

Webster, M. M., Atton, N., Hoppitt, W. J. E. and Laland, K. N. 2013. Environmental Complexity Influences Association Network Structure and Network-Based Diffusion of Foraging Information in Fish Shoals. - The American Naturalist 181: 235-244.

Weinrich, M. T. 1991. Stable social associations among humpback whales (Megaptera novaeangliae) in the southern Gulf of Maine. - Canadian Journal of Zoology 69: 3012-3019.

Wey, T., Blumstein, D. T., Shen, W. and Jordán, F. 2008. Social network analysis of animal behaviour: a promising tool for the study of sociality. - Animal Behaviour 75: 333-344.

White, L. A., Forester, J. D. and Craft, M. E. 2017. Using contact networks to explore mechanisms of parasite transmission in wildlife. - Biological Reviews 92: 389-409.

Whiting, M. J. and Greeff, J. M. 1999. Use of heterospecific cues by the lizard Platysaurus broadleyi for food location. - Behavioral Ecology and Sociobiology 45: 420-423.

Woolhouse, M. E. J., Taylor, L. H. and Haydon, D. T. 2001. Population Biology of Multihost Pathogens. - Science 292: 1109-1112.

Wright, J., Stone, R. E. and Brown, N. 2003. Communal roosts as structured information centres in the raven, *Corvus corax*. - Journal of Animal Ecology 72: 1003-1014.

Wu, Q., Fu, X., Small, M. and Xu, X.-J. 2012. The impact of awareness on epidemic spreading in networks. - Chaos: an interdisciplinary journal of nonlinear science 22: 013101.

Yang, H., Tang, M. and Zhang, H.-F. 2012. Efficient community-based control strategies in adaptive networks. - New Journal of Physics 14: 123017.

Zhang, C., Zhang, J., Weissing, F. J., Perc, M., Xie, G. and Wang, L. 2012a. Different reactions to adverse neighborhoods in games of cooperation. - PloS one 7: e35183.

Zhang, H., Small, M., Fu, X., Sun, G. and Wang, B. 2012b. Modeling the influence of information on the coevolution of contact networks and the dynamics of infectious diseases. - Physica D: Nonlinear Phenomena 241: 1512-1517.

Zhao, Y., Zheng, M. and Liu, Z. 2014. A unified framework of mutual influence between two pathogens in multiplex networks. - Chaos: An Interdisciplinary Journal of Nonlinear Science 24: 043129.

Zhou, J., Xiao, G., Cheong, S. A., Fu, X., Wong, L., Ma, S. and Cheng, T. H. 2012. Epidemic reemergence in adaptive complex networks. - Physical Review E 85: 036107.